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Programming of double-step saccade sequences: Modulation by cognitive control

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Abstract

The capacity to detect and correct errors is thought to engage cognitive control. To probe the nature of such control in relation to eye movements, subjects performed a double-step task under different instructions: to FOLLOW the appearance of successive targets; or to cancel the initial saccade and REDIRECT gaze to the final target location. Saccade sequences occurred in the FOLLOW and REDIRECT conditions where they represented correct and corrective behaviour, respectively. We observed that corrective responses were faster than correct responses, and concurrent preparation of saccades was facilitated during error correction. These results are consistent with psychological theories that posit supervisory cognitive control over action during error correction.
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1. Introduction

The hallmark of the voluntary control of action is the capacity to respond to changes that make current goals inappropriate. When confronted with such situations humans generally respond by inhibiting the ongoing action and programming another response appropriate to the new context. A paradigm used frequently to investigate such behaviour in the laboratory is the countermanding task (DeJong, Coles, Logan, & Gratton, 1995; Lappin & Ericksen, 1966; Logan & Cowan, 1984; Osman, Kornblum, & Meyer, 1986, 1990; Vince, 1948; reviewed by Logan, 1994), which has been adapted to probe the control of saccadic eye movements (Asrress & Carpenter, 2001; Cabel, Armstrong, Reingold, & Munoz, 2000; Hanes & Carpenter, 1999; Hanes & Schall,

1995; Kornyllo, Dill, Saenz, & Krauzlis, 2003; Logan & Irwin, 2000).

In the oculomotor version of the countermanding task subjects are instructed to make a saccade to the appearance of a peripheral target in the majority of trials. However, on a random fraction of trials called stop-signal trials following presentation of the target, the appearance of a “stop signal” which could be visual (Asrress & Carpenter, 2001; Hanes & Schall, 1995) or auditory (Colonius, Özyurt, & Arndt, 2001), serves as a cue to inhibit the pre-programmed saccade to the peripheral target. This ability is of considerable interest because it represents an internal act of control by which an overt movement is inhibited and has provided a fruitful approach to study neural basis of sensory (Hanes, Patterson, & Schall, 1998; Paré & Hanes, 2003) and cognitive (Ito, Stuphorn, Brown, & Schall, 2003; Stuphorn, Taylor, & Schall, 2000) control of gaze.

The basic ideas of countermanding can be also extended to probe how programmed movements maybe

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redirected rather than inhibited (DeJong et al., 1995). We have more recently trained monkeys to perform such a “redirect” task (Murthy, Thompson, & Schall, 2000, 2001; Sato, Murthy, Thompson, & Schall, 2001), which is a modified version of the classic double step task (e.g., Aslin & Shea, 1987; Becker & Jürgens, 1979; Komoda, Festinger, Philips, Duckman, & Young, 1973; Lisberger, Fuchs, King, & Evinger, 1975; Westheimer, 1954; Wheelless, Boynton, & Cohen, 1966). Here the appearance of the second peripheral target on infrequent random trials served as a “*redirect signal*” instructing the animal to cancel a pre-planned saccade and direct gaze to the location of the second target to obtain juice reward. Although monkeys were able to perform this task successfully most often, when monkeys failed to redirect their saccade to the new target, they made a sequence of two saccades: the initial erroneous saccade to the location of the original target followed by a second corrective saccade to the new target.

The present study using human subjects was motivated by the objective to study the programming of corrective saccades in more detail because a number of cognitive theorists have postulated executive or supervisory systems that oversee and modulate such behaviour during the programming of corrective actions (e.g., Baddeley, 1986; Botvinik, Braver, Barch, Carter, & Cohen, 2001; Logan, 1985; Meyer & Kieras, 1997; Norman & Shallice, 1986). Evidence in support of this concept of an executive system of control also derives from neuropsychological (e.g., Baddeley, 1986; Shallice, 1982), electrophysiological (Falkenstein, Hohnsbein, Hoormann, & Blanke, 1991; Gehring, Goss, Coles, Meyer, & Donchin, 1993; Holroyd, Dien, & Coles, 1998) and neuroimaging studies (Carter et al., 1998; Dehaene, Posner, & Tucker, 1994), where activity in the anterior cingulate and prefrontal cortices during the process of error correction has been shown to occur. In this study we specifically test whether the intervention of such a form of cognitive control occurs during the process of saccadic error correction.

In order to evaluate the effect of cognitive control during the programming of corrective saccadic eye movements, subjects performed a double-step task under different instructions: either to follow with successive saccades the target steps; or to cancel the initial saccade and redirect gaze to the final target (Fig. 3). While in both instances a sequence of two saccades were elicited, the second saccade in the FOLLOW condition constituted part of the *correct* response, but in the REDIRECT condition the second saccade was a *corrective* response following an error. Measurements of reaction times and intersaccadic intervals indicated that corrective saccades were programmed faster than the corresponding correct saccades resulting in faster saccade sequences consistent with the hypothesis that cognitive

control can facilitate the programming of the corrective response.

1.1. Programming of saccades sequences in REDIRECT and FOLLOW conditions

The oculomotor control underlying sequential behaviour of saccades has been explored in much detail (e.g., Becker & Jürgens, 1979; Findlay & Harris, 1984; Hallett & Lightstone, 1976a, 1976b; Hou & Fender, 1979; Komoda et al., 1973; Lisberger et al., 1975; Lévy-Schoen & Blanc-Garin, 1974; Wheelless et al., 1966) since the introduction of the double-step task by Westheimer (1954) in which single targets displaced to successive locations commonly results in the generation of a sequence of two saccades. The results of many such investigations demonstrate that the pause between the two saccades decreases and may fall below the normal reaction time as the temporal interval between the target displacement shortens, consistent with the hypotheses that two saccades may be programmed in parallel. In some instances the duration between two saccades can be short enough to result in single curved trajectory (e.g., Becker & Jürgens, 1979; Findlay & Harris, 1984; Minken, Van Opstal, & Van Gisbergen, 1993; McPeck, Han, & Keller, 2003; Van Gisbergen, Van Opstal, & Roebroek, 1987). These results show that although the generation of saccades is usually sequential, the processing of preceding saccades can occur in parallel. In the present study we explore how cognitive control modulates the extent of concurrent saccade preparation.

To evaluate the hypothesis that shorter reaction times in the REDIRECT condition reflected a greater capacity to process the second saccade in parallel with the first saccade, we used the framework described by Becker and Jürgens (1979) to assess the ability of the oculomotor system to program two saccades in parallel. Parallel programming occurs when the preparation of the second saccade, following the appearance of the second target, begins while the first saccade is being programmed and executed (Fig. 1). Note that although the scheme shown here describes the saccade programming in terms of a race model (Carpenter & Williams, 1995; Reddi & Carpenter, 2000) in which a steady rise in activation leads to initiation of the saccade when it reaches a threshold, the logic of the argument is not dependent on any particular architecture of the reaction time process. The extent to which parallel programming occurs depends on the interval between the appearance of the second target and the beginning of the first saccade, called the time delay (D). This is the time that is available to the saccadic system to reprogram the second saccade. From the logic of the parallel, independent saccade programming model it follows that the intersaccadic interval (ISI) should be inversely related to the delay with a slope of negative one (Fig. 1). In contrast, if the programming

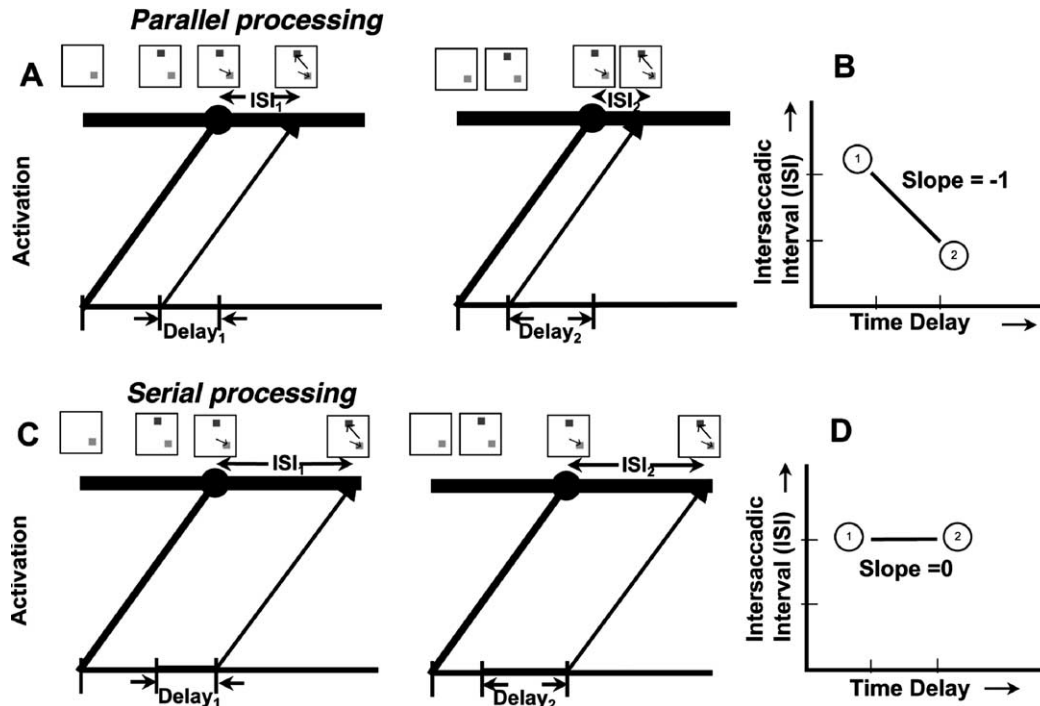


Fig. 1. (A) Schematic diagram showing the temporal sequence of events assuming the hypothesized parallel processing of two saccades. If the second saccade is programmed in parallel, longer time delays should produce shorter ISIs. (B) Ideal relation between ISI and time delay D during parallel programming of two saccades. The slope of the line should be negative one. (C) If two saccades are produced serially the length of the time delay D should not affect the ISI. (D) As a consequence there should be no relation between ISI and time delay (slope = 0).

of saccades were strictly serial, the preparation of the second saccade could begin only after the first saccade is executed. Consequently, the ISI would not vary with the delay, so the slope should be zero.

This framework can be extended to estimate the extent to which parallel processing ensues in a given interval (D_{2-1}) during the time delay period (Fig. 2). For example, if entirely independent parallel processing of the second saccade occurred during the interval, then the intersaccadic interval ISI should be reduced by an

amount equal to the time delay interval D_{2-1} . Consequently, the slope of the ISI as a function of step delay for saccades initiated during this interval should be equal to negative one. However, if processing of the second saccade is slowed during the interval D_{2-1} then the extent to which ISI is reduced should be less than D_{2-1} interval. Consequently, the slope of the ISI for saccades initiated during this interval should be, in absolute terms, less than one. Stated more generally, the slope of the plot of intersaccadic interval as a function of step

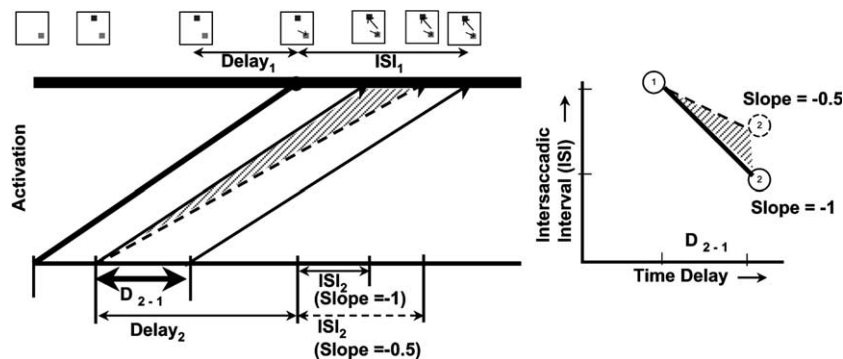


Fig. 2. The slope of the ISI versus time delay D function as a metric to estimate the rate of parallel processing during given interval. For simplicity, only two conditions corresponding to slopes or processing rates of -1 and -0.5 are shown. The time of stimuli and saccades are indicated schematically. If independent parallel processing of the second saccade occurred during the interval, the extent to which ISI is reduced should be equal to the delay interval D_{2-1} , yielding an ISI versus D_{2-1} slope of -1 . However, if the second saccade is processed at half its speed during the delay interval D_{2-1} , the extent to which ISI is reduced should be half the interval D_{2-1} , yielding an ISI versus D_{2-1} slope of -0.5 .

delay during this interval measures the extent of concurrent saccade preparation occurring during that interval. Thus, interpreted in this framework, the slope of the ISI in adjacent intervals during the time delay D can be interpreted as a metric describing the degree to which processing of the second saccade occurs while the first saccade is being programmed.

Using this approach, we demonstrate that the extent of parallel programming of saccades is influenced by the cognitive context in which saccade sequences are produced.

2. Methods

Nineteen naïve subjects with normal or corrected vision performed a visually guided saccade task while their eye movements were recorded with their heads stabilized by means of a chin rest. All subjects gave their informed consent in accordance with the institutional human ethics committee of National Brain Research Centre. Experiments were under computer control using TEMPO/VIDEOSYNC software (Reflective Computing, St. Louis, USA) that displayed visual stimuli and sampled and stored eye position and other behavioural parameters. Eye position was sampled at 200 Hz with an infra-red pupil tracker (ISCAN, Boston, USA) that interfaced with the TEMPO software in real time. All stimuli were presented on a Sony Trinitron 500 GDM monitor (21 in.; 70 Hz refresh rate) placed 57 cm in front of the subject. Stimuli were calibrated with a Minolta CA-96 colorimeter.

The task combines a standard saccadic reaction time task to single targets with a modified version of the double-step task (e.g., Aslin & Shea, 1987; Becker & Jürgens, 1979; Hou & Fender, 1979; Lisberger et al., 1975; Murthy et al., 2000) where two targets appear in succession on some trials. The double-step task was performed under two different instructions yielding two separate conditions: the FOLLOW condition and the REDIRECT condition. The temporal sequence of events that occurred in each type of behavioural condition and the resulting behaviour is shown in Fig. 3.

On the majority of trials (60%), referred to as *no-step trials*, following fixation for a random duration that ranged from 300 to 800 ms, subjects were instructed to make a saccade to a single target on its (1° by 1° green; 6.5 cd/m^2) appearance. The location of targets was randomized such that they could appear in any one of eight evenly spaced locations centred on an imaginary circle with a radius of 10° . For these trials subjects were also encouraged to respond quickly by imposing a 300 ms deadline to make the saccade.

On the remaining trials (40%), called *step trials*, following presentation of the first target (1° by 1° green; 6.5 cd/m^2), a second target (1° by 1° red; 6.5 cd/m^2) would appear unpredictably at another location on the screen (background luminance at 2 cd/m^2). For some subjects both targets were identical. Only those target steps were allowed in which the angular separation between the two targets was equal to or greater than 90° because a previous study (Ottes, Van Gisbergen, & Eggermont, 1984) indicated that larger angular separations encourages the production of sequences of two dis-

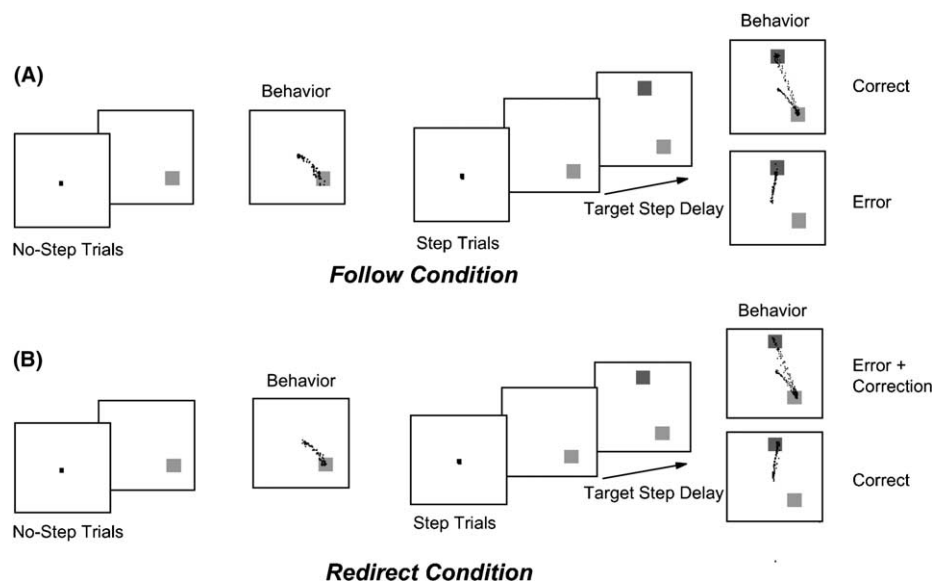


Fig. 3. Illustration of the temporal sequence of the stimuli and behavior in the FOLLOW (A) and REDIRECT (B) conditions. In the FOLLOW condition (A) subjects are instructed to direct their gaze to targets in their order of appearance. In the REDIRECT condition (B) subjects are instructed to cancel the pre-programmed eye movement to the initial target and direct gaze to the final target. In both conditions the step trials are interleaved randomly with no-step trials where a second target did not appear.

tinct saccades as opposed to single averaging saccade or a single curved saccade whose trajectory tracked the target step. The *target step delay*, the time of appearance of the second target relative to the first target, was varied randomly in steps of 50 ms. We used four target step delays of 49 ± 14 , 99 ± 14 , 149 and 199 ± 14 ms. For these trials no deadline was imposed to make the saccade.

Trials were scored as successful if subjects fixated the target within $\pm 2.5^\circ$. This was determined online by means of an electronic window centred on the target. Successful trials were accompanied by a sound that provided auditory feedback. The outcome of the trials was also scored on the computer to determine the magnitude of the monetary reward given to subjects at the end of the session.

In the step trials of the FOLLOW condition subjects were supposed to follow with successive saccadic eye movements the sequence of targets in their order of appearance. In the step trials of the REDIRECT condition subjects were supposed to cancel the programmed saccade to the first target and instead generate a saccade directly to the second target. Each subject performed the FOLLOW and REDIRECT conditions on separate days. Prior to each condition subjects were given written and verbal instructions with some practice trials (~ 50) before data was collected. On average subjects performed about 400–500 trials for each condition. These trials were run in batches consisting of approximately 100 trials each, with 10–15 min breaks in between batches. Most, subjects (12/19) performed the task under REDIRECT condition before the FOLLOW condition. However, for some subjects we switched the order of presentation. This did not have any effect on the data.

All offline analysis was performed using Matlab (Mathworks, USA). The analogue eye position data were smoothed from which blinks were removed. A velocity threshold of 30°/s was used to demarcate the beginning of saccades. The saccade detection algorithm was subsequently verified manually for every saccade. All blink-perturbed saccades were eliminated from analysis. All statistical tests were done using SigmaStat or Matlab.

3. Results

Fig. 3 illustrates the FOLLOW and REDIRECT conditions. During the FOLLOW condition subjects were instructed to make a sequence of two saccades to the target locations in their order of appearance. During the REDIRECT condition subjects were instructed to cancel the pre-programmed saccade to the first target location and generate a single saccade to the second target location. However, in many instances subjects failed to cancel the initial saccade directed to the first target location. Such incorrect responses were typically fol-

lowed by a corrective saccade to the specified target location. This pattern constituted a sequence of two saccades as in the FOLLOW condition. The analysis of the second saccade in both conditions provided the means to determine the effect of cognitive context, and in particular the role of error correction, on the programming of sequential saccades.

Fig. 4A illustrates the performance of a typical subject during the REDIRECT and FOLLOW conditions. In the REDIRECT condition when subjects were instructed to cancel the pre-programmed saccade, the probability of making a saccade directed at the initial target increased with target step delay. In contrast, during the FOLLOW condition the probability of making a saccade directed at the initial target was more or less independent of target step delay. This difference in performance is to be expected because the ability to cancel a partially prepared saccade diminishes with time, while following two targets does not require canceling the prepared saccade to the initial target. These differences in performances were quantified by fitting the best-fit cumulative Weibull function:

$$W(t) = \gamma - (\gamma - \delta) \cdot \exp(-(t/\alpha)^\beta)$$

where t is the target step delay; α is the time at which the function reaches 64% of its full growth; β is the slope; γ is the maximum value of the function and δ is the minimum value of the function. Since the term $(\gamma - \delta)$ describes the increase in the probability of making a saccade directed at the first target, we used it as an index to describe the monotonic dependence of the data as a function of target step delay and to quantify the degree of cancellation. Based on the described logic we expect data points of subjects to fall above the diagonal (Fig. 4B) corresponding to a cancel indices greater in the REDIRECT than in the FOLLOW conditions. Of the 19 subjects tested, 14 satisfied this criterion and were included for subsequent data analysis.

In addition to differences in performance, the general effect of cognitive context created by the different instructions could also be observed in the reaction times (RTs) of single saccades made during no-step trials. On average, the saccade were significantly longer (mean 216.3 ms) in the REDIRECT condition than in the FOLLOW condition (mean 180.3 ms; $P < 0.001$, 2-tailed t -test). This indicates that subjects on average adopted a more conservative strategy in generating saccades to single targets in the REDIRECT condition than in the FOLLOW condition (Fig. 4C).

To determine the influence of cognitive context on programming double-step saccade sequences we plotted the mean reaction times of the second saccade in the REDIRECT and FOLLOW conditions as a function of target step delay across the population (Fig. 5A). We also plotted the mean intersaccadic intervals (Fig. 5B) as a function of target step delay across the

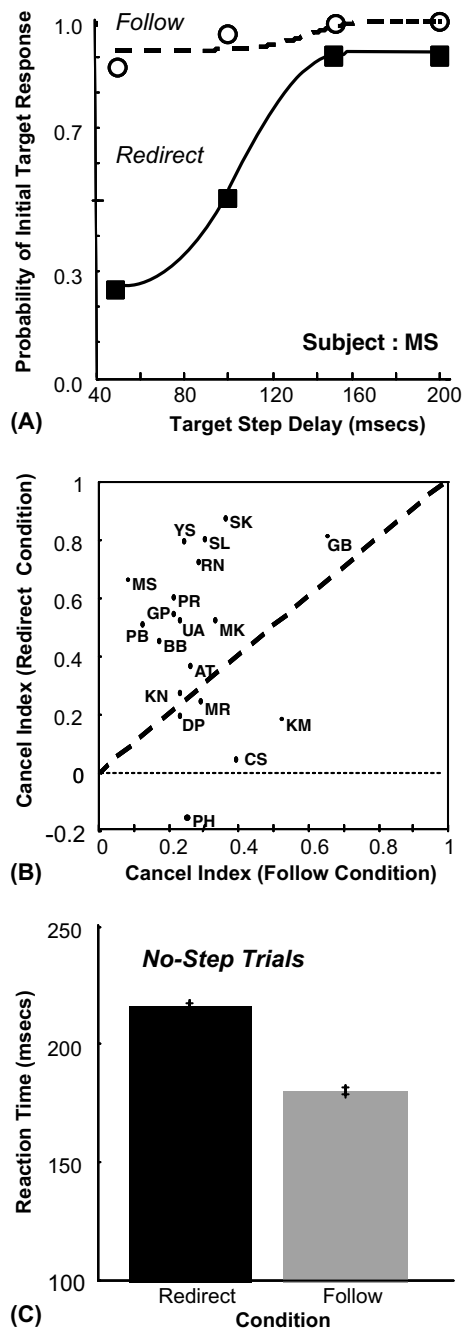


Fig. 4. (A) Performance of a subject in the FOLLOW and REDIRECT conditions. The probability of making a saccade directed at the initial target location is plotted versus the target step delay. The data points are fitted with the best fitting cumulative Weibull functions. (B) Scatterplot of the cancel index values derived from the Weibull function in the REDIRECT and FOLLOW condition for all subjects (see text for details). All data points falling above the diagonal were considered for subsequent analysis. (C) Mean RT during no-step trials were significantly longer in the REDIRECT condition than in the FOLLOW condition.

population. RTs and ISIs associated with the second saccade were significantly shorter in the REDIRECT condition than in the FOLLOW condition (mean RT

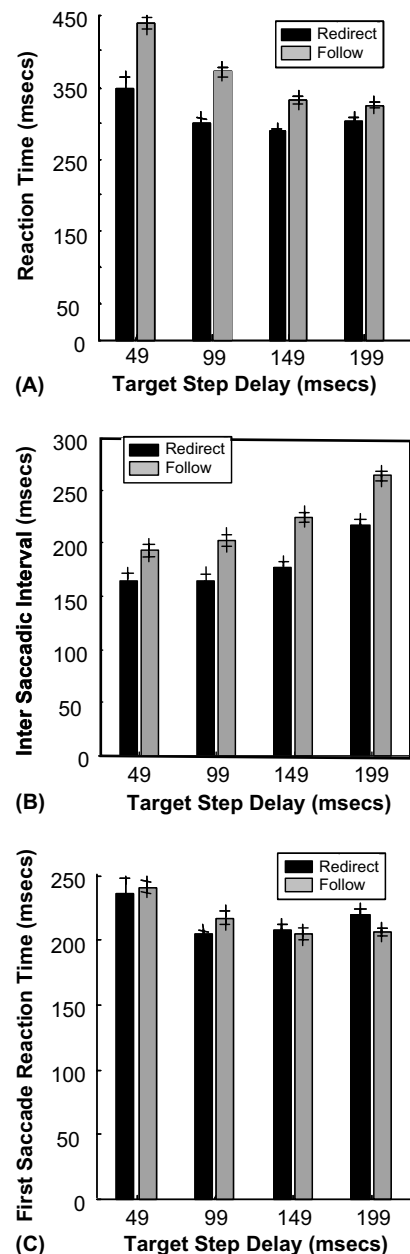


Fig. 5. (A) Mean RT for the second saccade during the REDIRECT and FOLLOW condition as a function of target step delay averaged across subjects ($n = 14$). The error bars denote the standard error of the mean. RTs are significantly shorter during the REDIRECT condition relative to the FOLLOW condition. (B) Mean ISIs observed in the FOLLOW and REDIRECT conditions plotted as a function of target step delay averaged across subjects ($n = 14$). The ISIs are shorter in the REDIRECT condition relative to the FOLLOW condition. (C) Mean RT for the first saccade during the REDIRECT and FOLLOW condition as a function of target step delay averaged across subjects ($n = 14$). RTs are not significantly different across the two conditions.

for REDIRECT = 310.5 ± 3.8 ms and FOLLOW = 366.4 ± 2.8 ms; mean ISI for REDIRECT = 181 ± 3.5 ms and FOLLOW = 220.9 ± 2.6 ms; two way ANOVA; $F(1,12) = 139.82$; $P < 0.001$ for RTs; and $F(1,12) = 84.36$; $P < 0.001$ for ISIs). The same was true even for

the remaining 5/19 subjects whose cancel indices were less in the REDIRECT condition relative to the FOLLOW condition (mean RT for REDIRECT = 340.5 ± 15.23 ms and FOLLOW = 424.2 ± 10 ms; mean ISI for REDIRECT = 200.6 ± 12.3 ms and FOLLOW = 239.2 ± 8.1 ms; two way ANOVA; $F(1, 3) = 21.07$; $P < 0.001$ for RTs; and $F(1, 3) = 7.01$; $P = 0.008$ for ISIs). This result was robust even at the level of individual subjects where 9/14 showed significantly shorter RTs (two way ANOVA, $P < 0.05$) and 9/14 showed significantly shorter ISIs (two way ANOVA, $P < 0.05$) in the REDIRECT condition relative to the FOLLOW condition.

Differences in the RT of the second saccade were not related to differences in RT of the first saccade, since these RTs were similar across the two conditions (mean in FOLLOW condition = 213.7 ± 1.8 ms; mean in REDIRECT condition = 211.7 ± 1.9 ms; two way ANOVA $F(1, 12) = 0.0019$, $P = 0.965$; see Fig. 5C). We also ruled out speed accuracy tradeoffs as being the cause for shorter second saccade reaction times. A Multivariate Analysis of Variance (MANOVA) revealed no statistically significant difference ($P = 0.504$) in the distribution

of saccade end points between the two conditions across different target positions.

In addition to the faster reaction times observed for the corrective saccade relative to the correct saccade, we also examined the effect of cognitive context on the ability of the oculomotor system to program saccades concurrently. Fig. 6 illustrates the data from nine representative subjects. The ISI and time delay D for each trial yielding sequential saccades (errors in REDIRECT and correct in FOLLOW conditions) were computed as in Figs. 1 and 2. The time delay intervals were binned into uniform intervals of 50 ms from which the means and standard errors were computed. The corresponding values of ISIs were averaged to compute the mean ISI and standard error. Data points corresponding to bins with less than five trials were not included, as they were considered unreliable. Note that time is inverted on the time delay axis with shorter D 's reflecting later instances in time.

Despite individual variability, three distinct trends were observed. First, ISIs tends to decrease with time delay D indicating some degree of parallel programming occurred in both conditions. Second, the function

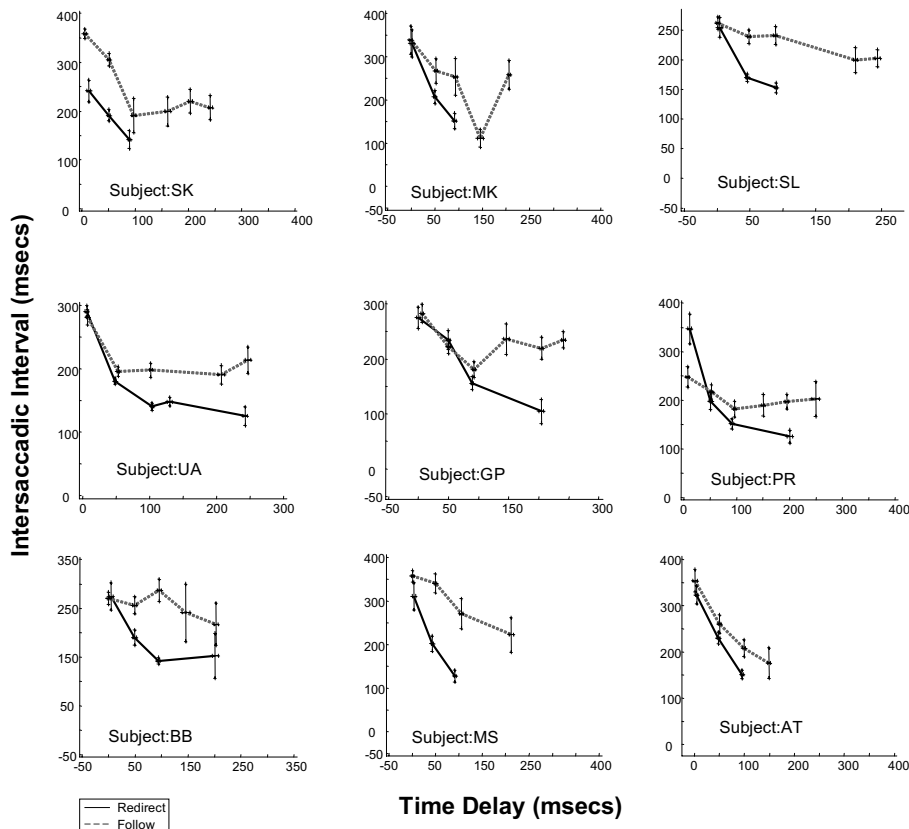


Fig. 6. Plots of ISI versus time delay D for nine representative subjects in the REDIRECT (black lines) and FOLLOW (grey lines) conditions. In general, the function characterizing the ISI vs. D function in both conditions monotonically decreases to a point beyond which ISIs are relatively independent of delay. The ISI versus delay function is steeper in the REDIRECT condition relative to the FOLLOW condition. Error bars in the graph denote the standard error of the mean.

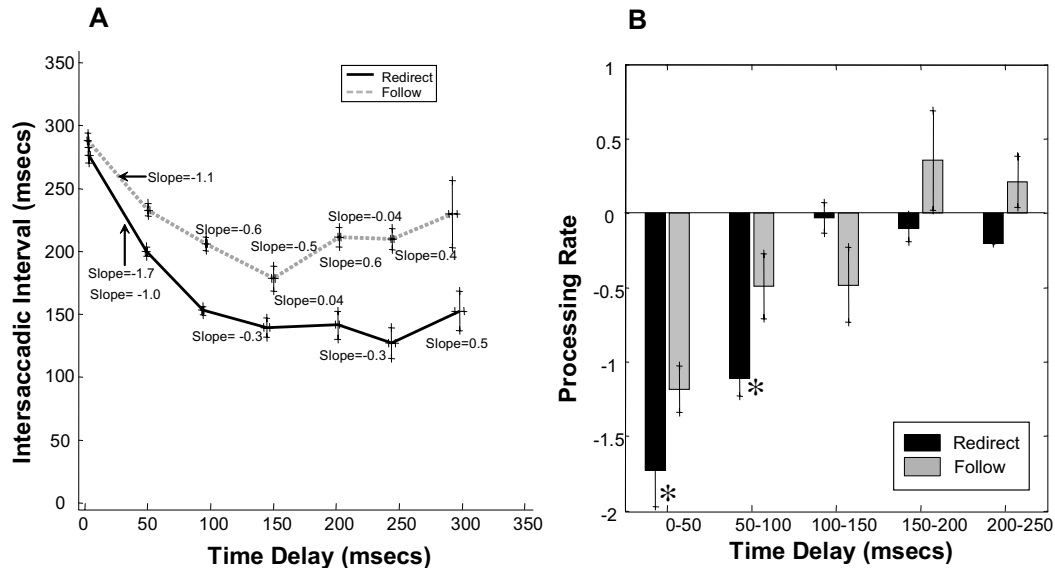


Fig. 7. Population response. (A) In both conditions ISIs decrease as a function of D consistent with parallel programming. However, the average rate of decrease is greater in the REDIRECT condition suggesting facilitation of parallel programming relative to the FOLLOW condition. The values denote the slopes or processing rates of corresponding line segments. Error bars denote the standard error of the mean. (B) Histogram distribution of the slopes describing the processing rate as a function of D . Error bars denote the standard error of the mean. Asterisks denote significant (pair wise t -test $p < 0.05$) differences between the conditions.

characterizing the ISI versus D relation can be approximated by a series of line segments joining adjacent data points, whose slopes tend to decrease progressively with increasing delay up to a minimum. Since the slope of the line segments can be considered a metric that represents the rate of processing of the second saccade during the delay interval, such a pattern indicates that the degree of parallel processing diminishes with increasing delays up to a point, beyond which processing appears to be serial. Stated differently this implies that at the longest delay intervals there is little or no processing of the second saccade; consequently ISIs do not decrease. Third, and most important from the perspective of this study, is that processing rates are faster in the REDIRECT condition than in the FOLLOW condition. This is particularly prominent at the shorter time delays.

Fig. 7A illustrates the same trends across the population. The processing rates for each delay interval are also shown. ISIs in the REDIRECT condition decrease from 276 to 139 ms yielding an average processing rate of -0.97 , whereas ISIs decrease from 288 to 178 ms yielding an average processing rate of -0.74 in the FOLLOW condition. Since the ISIs corresponding to the first bin at the delay of 0 ms are similar in both REDIRECT and FOLLOW conditions it follows that the shorter ISIs in the REDIRECT condition must be explained largely by the greater processing rates that lead to successively larger differences in ISI across the conditions. A similar explanation can account for the differences between the ISIs in the two conditions even in the majority of individual subjects (see Fig. 6).

A more detailed analysis of the processing rates as a function of time delay D is illustrated in Fig. 7B reiterating the result that slopes are significantly steeper in the REDIRECT condition than in the FOLLOW condition up to 100 ms (one-way t -test, $t = 1.752$, $P = 0.046$ for the first delay; and $t = 2.45$, $P = 0.011$ for the second time delay interval). From 150 ms onwards the processing rates are not different from each other or significantly different from zero in either condition. Interpreted within the logic of the framework outlined, these data indicate that parallel programming is facilitated in the REDIRECT condition relative to the FOLLOW condition, giving rise to faster saccadic sequences in the REDIRECT condition. Interestingly the processing rates corresponding to the delay bin between 0 and 50 ms in the REDIRECT condition are significantly steeper than negative one (t -test, $t = 2.712$, $P = 0.01$), suggesting a facilitation of parallel programming above and beyond that expected from a temporal overlap of two saccade programs.

4. Discussion

In the present study we demonstrated that corrective saccades following errors in the REDIRECT condition were faster than the corresponding correct saccade in the FOLLOW condition. By extending the analysis of Becker and Jürgens (1979) we also provided evidence that the parallel programming of saccades is facilitated in the REDIRECT condition relative to the FOLLOW

condition. Taken together our results support the notion that cognitive control exerted during the occurrence of errors may assist in the concurrent processing of the corrective saccade, resulting in faster reaction times and shorter intersaccadic intervals.

Before discussing the functional implications of these findings we evaluate the premise that by instructing subjects prior to the experiment to either follow the sequence or redirect gaze from the first to the second target, we generated different cognitive contexts in the FOLLOW and REDIRECT conditions such that correct performance in one context was incorrect in another context, enabling us to probe the contribution of cognitive mechanisms that are activated during the making and correction of errors. Based on the instructions were such different cognitive contexts elicited? We believe this premise to be justifiable on two grounds. First, examination of the subjects' performance, as quantified in the Weibull function, differed in accordance with the instructions. The majority of subjects tested displayed higher Cancel Index (C.I.) values in the REDIRECT condition than in the FOLLOW condition. This follows logically, since the ability to cancel a pre-programmed saccade should diminish with time, or target step delay, leading to higher C.I. values. Second, reaction times in no-step trials were significantly greater in the REDIRECT condition than in the FOLLOW condition. Delaying the initiation of saccades in no-step trials in the REDIRECT condition is likely to reflect the intervention of a form of cognitive control as a consequence of errors accrued during previous trials. The same phenomenon has also been observed in monkeys performing similar tasks (Sato et al., 2001; Schall & Taylor, 1998). In fact such increases in reaction times following errors formed the original behavioural evidence for a supervisory control system (Rabbitt, 1966; Rabbitt & Phillips, 1967) that serves to minimize the occurrence of subsequent errors, and can be construed of as another manifestation of error correction with a slower time course.

In contrast to assuming the intervention of cognitive control during error correction in the REDIRECT condition that facilitates saccade programming, can the observed differences in reaction times and parallel programming reflect a general slowing in the programming of saccade sequences during the FOLLOW condition? For the following reasons we do not think this can explain the observed results. First, evidence for parallel programming was obtained for subjects performing the FOLLOW task suggesting that they did not simply delay their second saccades. Second, the data for a number of individual subjects (Fig. 6) and for the population response (Fig. 7) indicates that at the shortest time delays the ISIs for REDIRECT and FOLLOW were comparable and not significantly different from each other. This pattern is not expected if subjects simply chose to delay

their second response in the FOLLOW condition. Third, the second saccades in the FOLLOW condition were not any more accurate than the corrective saccades as might be the case if subjects adopted a more conservative strategy in the FOLLOW condition. Taken together we interpret the pattern of behaviour as favouring the hypothesis that shorter RTs and ISIs in REDIRECT reflect facilitation of saccade programming as opposed to being a consequence of a general slowing of saccade programming in the FOLLOW condition.

4.1. Modulation of parallel programming during error correction

The functional implications of our findings are considered in relation to previous work describing parallel programming of saccades. We focus on the data of Becker and Jürgens (1979) since our analyses of parallel programming derives conceptually from their analyses; unlike other double-step studies for which the focus was on other aspects of oculomotor control such as the ability of the oculomotor system to respond to new visual input (e.g., Hou & Fender, 1979; Komoda et al., 1973; Westheimer, 1954); the coordinate transformations used by the oculomotor system (e.g., Dassonville, Schlag, & Schlag-Rey, 1995; Goldberg & Bruce, 1990; Guthrie, Porter, & Sparks, 1983; Hallett & Lightstone, 1976a, 1976b; Honda, 1989) or as a paradigm to test the adaptive properties of the oculomotor system (e.g., Deubel, Wolf, & Hauske, 1986).

Our findings from the REDIRECT condition, which is analogous to the instructions given to subjects in the Becker and Jürgens (1979) study, confirm the earlier observations showing an inverse relationship between ISI and time delay D . As in their data we also observed that the relationship between ISI and D reached an asymptotic value. In our data this occurred within 150 ms beyond which the relationship was flat. However, unlike the idealized relationship (see Fig. 2; or see Fig. 7 of Becker & Jürgens, 1979) the function between experimentally observed ISI and D cannot be characterized as being linear with a slope of negative one, but is nonlinear. Although such a function is more naturally described by an exponential relation we used line segments instead of a single exponential because it fits into the theoretical framework of the ISI versus D relation. Using line segments allows a functional interpretation of the slopes values not directly possible with exponents; the caveat to this analysis being that the processing rates represents an average across 50 ms time intervals.

The observation that concurrent preparation rates decrease with time delay implies that the greater overlap between two saccadic programmes, the slower is the processing of the second saccade. Conceivably this may be due to reduced speed of processing when there is sharing of common resources. A similar slowing of

processing speeds is also observed in dual task paradigms where the second task exhibits a psychological refractory period that is thought to reflect sharing of limited resources or the presence of a processing bottleneck (e.g., Pashler, 1984; Pashler, Carrier, & Hoffman, 1993; Welford, 1952). While this view can account for processing rates smaller than the ideal (negative 1.0), they fail to account for instances where the processing rate is steeper than negative 1.0. A strict interpretation based on the logic of parallel programming indicates that these values could reflect recruitment of processes that facilitate parallel programming of the second saccade beyond that expected from temporal overlap.

Alternately, a functional interpretation of these slopes might be limited due to response variability in the ISI– D relation, which may be considerable. However, this appears not to be the case for the following reasons. First, processing rates steeper than negative 1.0 were invariably associated with the REDIRECT condition at the shortest time delays and not randomly distributed. This could be observed in the population response (see Fig. 7B) as well as in the response of individual subjects where in 11/14 subjects the processing rates associated with the shortest time delay interval were steeper than -1.0 . Second, the shortest delays associated with the highest slopes or processing rates mark the time intervals where the difference between the two conditions reached statistical significance. Taken together such a systematic pattern of processing rates suggests that prior to the initiation of the first saccade there is a facilitation of parallel programming that occurs in the REDIRECT condition. The functional implication of this is discussed further.

4.2. Cognitive control during error correction

A key difference between the second saccade in the REDIRECT and FOLLOW conditions is the context in which they are generated. Since subjects in the REDIRECT condition were instructed to cancel the partially prepared saccade to the first target, the second saccade is a corrective saccade following the occurrence of an error. In contrast, the second saccade in the FOLLOW condition occurs as part of the correct response. Thus, faster reaction times of the second saccade in the REDIRECT condition may reflect the influence of an error correction system that facilitates the programming of corrective saccades (Schall, Stuphorn, & Brown, 2002). Since some of this facilitation appears to be engaged in parallel with the erroneous saccade as reflected in the steeper slopes of the ISI versus D function, a logical inference is that our brain may possess the capacity to predict the likely occurrence of an error and begin programming the forthcoming action that will correct it. Potentially this could involve the use of internal feedback control that is feature of numerous oculomotor

control models (e.g., Becker & Jürgens, 1979; Robinson, 1968; Scudder, 1985) as well as feedforward control in error correction systems (e.g., Bernstein, Scheffers, & Coles, 1995; Desmurget & Grafton, 2000; Shadmehr & Mussa-Ivaldi, 1994; Wolpert, Ghahramani, & Jordan, 1995). Here error correction is implemented by a comparison of an internal goal or desired displacement with an efferent copy of the motor command. Any deviations can be corrected without the requirement for delays associated with sensory feedback. In principle such a mechanism allows for error correction to proceed even before the error is committed.

However, an alternative interpretation is that the facilitated preparation of the second saccade in the REDIRECT condition might reflect differences in the nature of the stimuli in the two conditions. Unlike the FOLLOW condition, the second target in the context of the REDIRECT condition serves as an imperative interrupt or stop-signal (Asrress & Carpenter, 2001; Hanes & Carpenter, 1999; Hanes & Schall, 1995) with potentially higher priority. As a consequence the second target might engender a greater allocation of attentional resources than the corresponding second target in the FOLLOW condition. In light of the observed links between attention and saccade programming (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler, Anderson, Doshier, & Blaser, 1995; Shepherd, Findlay, & Hockey, 1986), greater allocation of attention could translate into faster visual processing speeds (Carrasco & McElree, 2001) that may facilitate the corrective saccade. Although this hypothesis is distinct from the error correction hypothesis in that facilitation of saccade programming is attributed to the nature of the stimulus as opposed to the type of response, the two hypotheses are not mutually exclusive. Rather they can be seen as the workings of a higher order executive control mechanism (e.g., Baddeley & Della Sala, 1996; Botvinik et al., 2001; Logan & Gordon, 2001; Shallice & Burgess, 1996) that optimises oculomotor behaviour depending on task conditions.

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